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Are ground beetles neutral?

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Nestedness;
Colonisation

Summary

The neutral model approach to community ecology is currently intensively discussed but has mainly been tested for its ability to mimic observed patterns like species–abundance or abundance–occupancy distributions. Less well studied is the question whether neutral models are able to explain these distributions and other ecological patterns like species co-occurrences simultaneously. Here we use a random draw and a spatially explicit neutral model to test whether both models are able to predict patterns of island colonisation by ground beetles. We show that island colonisation is not a simple random draw from the mainland metacommunity. The neutral model was able to mimic basic patterns of species diversity, island occupancy, and island abundances. Both models, however, were unable to produce observed non-random patterns of species co-occurrences and nestedness while predicting random distributions of species across islands. The neutral model produced patterns of nestedness and abundance–occupancy relationships that were intermediate between the observed patterns and the predictions from a simple random draw. Our results add further to the view that a neutral model might be the appropriate null model for the study of ecological communities. Its ability to mimic basic patterns of biodiversity helps to sharpen our perception of niche differences and competitive effects that might cause deviations from the model. It seems better suited to distinguish between random effects and species interactions than simple random draw models.

Zusammenfassung

Neutrale Gemeinschaftsmodelle werden derzeit intensiv diskutiert, wurden aber im Wesentlichen nur in Bezug auf Abundanzverteilungen und Abundanz–Verbreitungsverteilungen getestet. Weniger gut geklärt ist die Frage, ob neutrale Modelle diese und andere makroökologische Verteilungen simultan beschreiben können. In dieser Arbeit benutzen wir ein einfaches Zufallsmodell sowie ein räumlich explizites

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neutrales Modell um zu testen, ob beide in der Lage sind, die Artenverteilungen von Laufkäfern auf kleinen Inseln zu erklären. Wir zeigen, dass Kolonisation keine einfache Zufallsauswahl aus einer Metagemeinschaft darstellt. Unser neutrales Modell hingegen beschrieb Kolonisation, Diversität und Abundanzen korrekt. Beide Modelle waren jedoch nicht in der Lage beobachtete Muster des gemeinsamen Auftretens von Arten sowie der Artenschachtelung zu generieren. Das neutrale Modell kam dabei den beobachteten Verteilungen näher als das reine Zufallsmodell. Wir folgern daraus, dass neutrale Modelle in der Tat geeignete Nullmodelle bei der Analyse von Gemeinschaftsstrukturen sein können. Ihre Fähigkeit einfache ökologische Verteilungen zu simulieren, kann unseren Blick für Nischendifferenzierungen und Wettbewerb schärfen. Darin sind neutrale Modelle einfachen Zufallsmodellen überlegen.

Introduction

The neutral model approach to community ecology proposed by Hubbell (1997, 2001), McKane, Alonso, and Solé (2000), and Bell (2001) is recently one of the most intensively discussed ecological theories (Bell, 2005; Chave, 2004; Etienne, 2005; Etienne & Olff, 2004; Etienne & Alonso, 2005; Gotelli & McGill, 2006; Ulrich, 2004a). According to the most elaborate of these approaches, the ecological drift model (EDM) of Hubbell (2001), local communities have a fixed number of individuals (the carrying capacity) and are assembled (irrespective of species membership) by simple birth and death processes, dispersal, and speciation. Speciation is the main driver of the distribution of abundances in the metacommunity. Neutral models dismiss therefore the classical assembly rule models of community structure (Diamond, 1975). In particular, they do not discern between intra- and interspecific competition and lack any density dependant population regulation (Chave, Muller-Landau, & Levin, 2002; Hubbell & Lake, 2003). They challenge therefore the classical competition centred paradigm of community ecology (Chave, 2004; Golley, 1993; Ulrich, 2004b; Weiher & Keddy, 1999).

Tests of neutral models centred mainly on single ecological distributions and found that neutrality alone is able to fit observed patterns of species–abundance distributions (SAD) (Pitman et al., 2001; Volkov, Banavar, Hubbell, & Maritan, 2003), abundance–range size distributions (Condit, Pitman, Leigh, Chave, Terborgh et al. 2002), species–area relationships (Hubbell, 2001), and patterns in evolutionary lineages (Webb & Pitman, 2002) although for each of these 'successes' counter-examples exist (Enquist, Haskell, & Tiffney 2002; Fargione, Brown, & Tilman, 2003; Ricklefs, 2003; Ulrich & Ollik, 2004). In particular, recent investigations (Bell, 2005; Ulrich, 2004b) found EDM to produce non-random patterns of species co-occurrences similar to those proposed by assembly rule models (Diamond, 1975; Gotelli & McCabe, 2002). However, it becomes more and more clear that, to be successful, neutral models must predict the mentioned patterns (and potentially others) of community structure simultaneously (Adler, 2004; Ulrich, 2004a; Ulrich & Ollik, 2004) because for single distributions a sufficiently flexible model like EDM with at least four free parameters (species pool size, birth/death rate, dispersal limitation, speciation rate) will often fit observed data.

One aspect of community assembly that received little attention in the discussion around neutral models is island biogeography. The modelling of island colonisation requires spatially explicit models that are difficult to fit to observed patterns and have to be based on extensive simulations (Chave, 2004). Further, it needs data on the structure of the metacommunity that serves as the source pool of colonisation. These difficulties might explain why there is to date no explicit test to check whether EDM is able to mimic observed patterns of species occurrences on islands. The present paper aims to do this. It uses data of the distribution of 71 ground beetle species on 15 small lake islands in Mamry lake in Northern Poland and the surrounding mainland (Ulrich & Zalewski, 2006; Zalewski, 2000, 2004; Zalewski & Ulrich, 2006). This dataset is exceptionably suitable for testing the predictions of neutral model approaches because it contains detailed data on island occupancy and abundances. Previous studies showed that the ground beetle communities can be divided into groups of core and satellite species and into groups of different dispersal ability (macropterous, dimorphic and brachypterous). These groups differ in important macroecological patterns like species–area relationships (SARs), SADs and abundance–occupancy

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distributions (AODs) (Ulrich & Zalewski, 2006; Zalewski & Ulrich, 2006). It is therefore important to see whether ecological drift is able to mimic these differences between ecological groups.

We consider two types of neutral models. First, we test a colonisation process that is solely driven by migration. Hence, individuals (irrespective of species) colonise islands from the mainland and migrate between islands at a predefined dispersal probability p. Such a model is equivalent to a random assortment of species per island according to the relative abundances of the metacommunity (termed the RAM model below). It has only one free parameter, the migration probability that defines how fast a stable pattern is achieved. The model is a multi-patch equivalent to the random draw model of Dolman and Blackburn (2004), who studied the avifauna of a British woodland in comparison to the species pool of British birds.

Second, we include birth and death processes (triggered by the birth/death probability q). This spatially explicit two-parameter EDM can be fitted to various aspects of community structure, for instance to the observed SAD, to the SAR, or to the AOD. In our view, any model should basically predict observed species numbers. Hence, we use this criterion to adjust the parameters p and q to get an EDM that best predicts the observed numbers of species per island. This criterion is equivalent to a best fit to the observed SAR. In the following, we use RAM and EDM to see whether observed patterns of island community structure can be described by a simple random draw of species, by ecological drift, or whether observed patterns deviate from both models.

We consider six basic patterns of community structure. First we study the possible distinction into core and satellite species as well as SARs and AODs, since these are distributions mainly based on species richness. We further use SADs to infer whether RAM and EDM are able to mimic observed island abundances. Finally, we study whether RAM and EDM predict observed patterns of species co-occurrence and nestedness.

Materials and methods

Fifteen island and two forested mainland sites (variants of *Tilio-Carpinetum* and *Carici elongatae-Alnetum* associations) from the largest archipelago of islands in Poland in the Mazurian Lake Mamry (21°30′–21°52′E, 54°00′–54°10′N) were sampled using pitfall traps (0.5 l plastic mug, mouth diameter 120 mm, wooden roof). Between 2 and 21 traps were used per site, depending on its habitat diversity and size making up a total of 107 traps. Traps operated from June to September 1997 and 1998 and were emptied monthly and refilled with fresh glycol (Zalewski, 2000).

All carabid species except the genus *Europhilus* were identified to species level using the keys of Hürka (1996) and Lindroth (1985). Nomenclature follows Hürka (1996). Life history and morphological characteristics are based on Den Boer, van Huizen, den Boer-Daanje, Aukma, and den Bieman (1980), Lindroth (1985), and Hürka (1996). Complete species lists, abdundances, and island occupancies are contained in Ulrich and Zalewski (2006). The classification into core and satellite species follows Ulrich and Zalewski (2006), the grouping into macropterous, dimorphic, and brachypterous species follows Zalewski and Ulrich (2006).

To study whether ecological drift is able to mimic observed patterns of species distribution across islands we constructed a grid of 16 cells of which 15 cells represented the 15 islands to be colonised and one the mainland. The mainland cell served as the metacommunity and contained all 71 species observed according to their relative abundance in the two mainland sites sampled. The number of individuals of this metacommunity was set to infinity. The island cells were initially empty. The present EDM model is now a multi-patch version of Hubbell's (2001) ecological drift model without speciation. It contains three steps that were repeated 7,500,000 times (enough to result in a stable pattern; Fig. 1):

1. Pick an individual (irrespective of species identity) with a predefined dispersal probability p from one of the 16 cells at random and let it migrate to another randomly chosen cell.
2. Pick an individual (irrespective of species identity) with a predefined birth probability q from one of the 15 island cells at random to give birth to another individual of the same species. Because the number of individuals of the mainland cell was set to infinity we did not play the birth/death game for this cell.
3. Pick an individual (irrespective of species identity) with a predefined death probability q from one of the 15 island cells at random and let it die.

This process results in an accumulation of individuals in the initially empty island cells. For cells that reached the observed number of individuals (these numbers served as carrying capacity K and are contained in the second and third panel of

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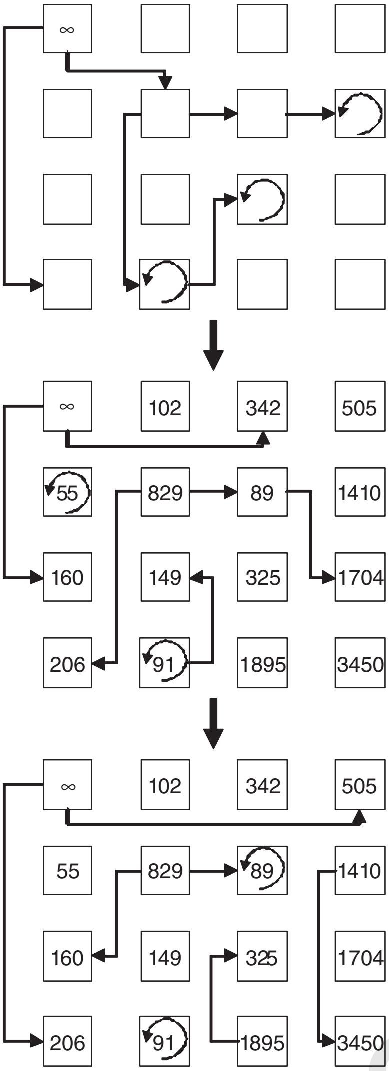

Figure 1. Graphical scheme of the modelling process. Individuals colonised islands from a mainland metacommunity and migrated between islands at random according to a predefined dispersal probability. On each island, births and deaths occurred according to a predefined birth/death probability. Islands accumulated individuals until the observed number of individuals was reached (the numbers in each cell, cf. Ulrich & Zalewski, 2006). Afterwards for this island the zero sum multinomial was run. The whole process was continued until in total 7,500,000 emigrations, immigration, births, and deaths had taken place. Arrows denote dispersal, arrows within cells birth and death processes. The ordering of the cells in the grid reflects roughly the distance from the nearest mainland.

Fig. 1) individual numbers were held constant according to the zero sum multinomial. Each immigration or birth was immediately counterbalanced by a death and each emigration or death counterbalanced by a birth.

In the RAM approach the birth/death probabilities *q* were set to 0. Hence, species accumulation was solely driven by migration and resulted in a simple random draw of species according to mainland relative abundances.

Island distances and distances from the nearest mainland appeared to be only weak predictors of species occurrences (Ulrich & Zalewski, 2006; Zalewski & Ulrich, 2006). Hence, we did not include island distances in the model. Nevertheless, we assumed no dispersal limitation for macropterous and dimorphic species and dispersal only to the nearest cells for brachypterous species. Confidence limits were inferred from 100 replicates of the best-fit model.

Our measure of goodness of fit was the mean number of species per island. We repeated the model runs each time adjusting the parameters *p* and *q* until the model mimicked the observed species numbers best. These parameters were then used for all further modelling.

We used *C*-scores (Stone & Roberts, 1990), checkerboard scores (Gotelli, 2000), and species combination scores (Pielou & Pielou, 1968) to compare observed species co-occurrences with those obtained from EDM and RAM. The *C*-score and the checkerboard score measure matrix wide species underdispersion (checkerboard patterns), the species combination score by contrast screens for unique species combinations (Gotelli, 2000). Random matrices for generating standardized (*Z*-transformed) effect sizes with a mean of zero and a variance of one and significance levels (based on 5000 replicates) were computed with EcoSim 7 (Gotelli & Entsminger, 2006) using fixed sum row and column constraints and the sequential swap algorithm for randomisation. Significant species underdispersion or overdispersion, on the other hand, should result in *Z*-transformed scores above 1.96 or below −1.96 (at the 5% error level).

We further used the nestedness temperature calculator (Atmar & Patterson, 1995) to infer whether both models resulted in a nested pattern of cell colonisation (whether the faunal composition of different study sites form perfect subsamples from the larger common species pool) and whether the model distributions differed from the observed ones. The calculator computes a measure of nestedness (the matrix temperature *T*) and compares this with a T_{null} value obtained from a random distribution of species among sites (using a built in randomisation procedure without column and row constraints, cf. Wright, Patterson, Mikkelson, Cutler, & Atmar, 1998).

To estimate evenness we used Simpson's index ($D = 1 - \Sigma p_i^2$, with p_i being the relative abundance of species i; cf. Olszewski, 2004). We used *Statistica* 7.1 (StatSoft, 2005) for standard statistical analysis. Regression functions refer in all cases to estimates of the programs' non-linear estimation module (model I least squares, Levenberg–Marquardt estimation). The program *NeutralCom*, with which we simulated the models, is available at the homepage of WU (www.uni.torun.pl./~ulrichw). If not mentioned otherwise standard errors are given with means.

Results

EDM fitted best at $p = 0.1$ and $q = 0.0009$ where it exactly predicted the mean number of species S per island (mean $\Delta S = (S_{\text{predicted}} - S_{\text{observed}}) = 0 \pm 1.37$). On the other hand, RAM consistently overestimated island species numbers (mean $\Delta S = (S_{\text{predicted}} - S_{\text{observed}}) = 6.1 \pm 1.49$). Accordingly, observed and EDM predicted SARs were nearly identical (Fig. 2). When fitted by the power function SAR model, slope and intercept values did not significantly differ (Fig. 2; $p(t) > 0.1$). The slope of the RAM SAR did also not significantly differ from both other slopes (Fig. 2). The RAM intercept, on the other hand, was significantly higher than both the observed and the EDM one (both $p(t) < 0.001$). For the two models, there was no detectable trend in ΔS with respect to island area (all regressions of ΔS on A not significant at the 5% error level).

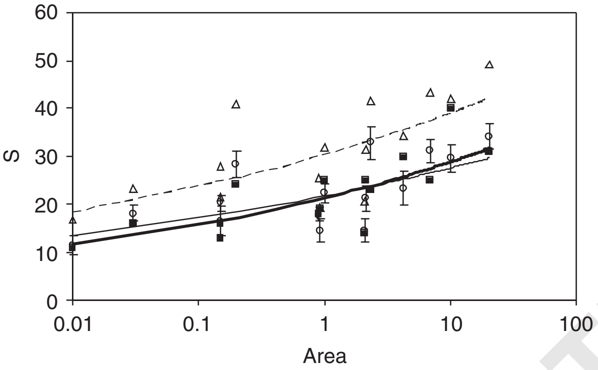

Figure 2. SARs of all carabid species. Open triangles: Mean species numbers per island of RAM. Open circles: Mean species numbers of EDM (error bars denote one standard deviation). Black squares: Observed species numbers. Error bars of the random model are left out to ensure readability. Regression lines: bold line (observed SAR): $S = (20.6 \pm 1.4)A^{(0.13 \pm 0.03)}$; $R^2 = 0.62$; light line (EDM): $S = (22.2 \pm 1.5)A^{(0.11 \pm 0.03)}$; $R^2 = 0.46$; broken light line (RAM) $S = (30.9 \pm 2.0)A^{(0.12 \pm 0.03)}$; $R^2 = 0.52$. S: number of species, A: area in ha.

Further, the ground beetles of lake Mamry showed a marked logarithmic AOD (Fig. 3A). Both models were able to mirror this relationship (Fig. 3B and C). However, in the mean EDM produced a scatter of data points (measured by the coefficient of determination) around the logarithmic regression line ($R^2 = 0.82 \pm 0.01$; errors estimated from the 100 replicates) that was again intermediate between the RAM prediction ($R^2 = 0.86 \pm 0.01$) and the observed scatter ($R^2 = 0.79$).

Previously we found (Ulrich & Zalewski, 2006) that the ground beetles could be separated into core and satellite species when using $\log_2$ island occupancy classes. Defining satellite species as those that occupied only one island (the first class in Fig. 4) and core species as those that occupied more than eight islands (the last column in Fig. 4) it appeared that both groups were fitted by different SADs and differed also in species co-occurrences. Both RAM and EDM also produced a core–satellite pattern (Fig. 4). However, RAM predicted significantly lower satellite and higher core species numbers than observed ($p(t) < 0.01$) whereas the EDM pattern did not significantly differ from the real one ($p(t) > 0.1$).

These differences are mirrored in the respective SADs. SADs predicted by EDM were for core and satellite species nearly indistinguishable from the

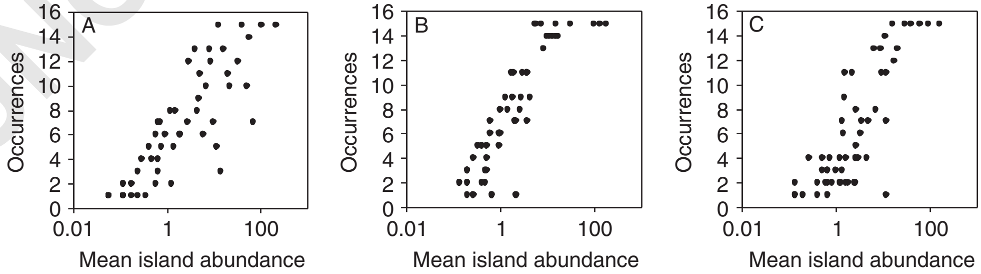

Figure 3. Observed abundance–occupancy relationships of the 71 ground beetles (A) and typical AODs predicted by RAM (B) and EDM (C). Abundances are mean numbers of individuals per occupied island; occurrences denote the numbers of islands occupied.

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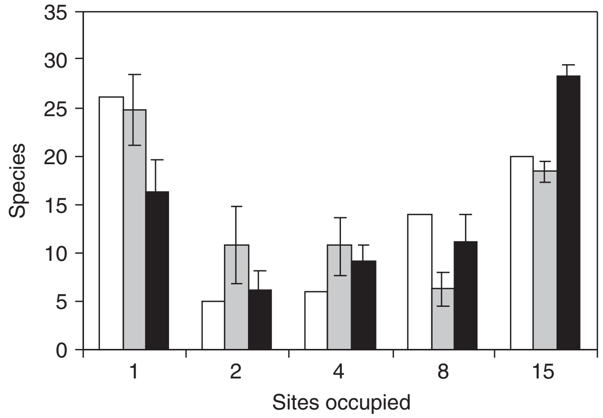

Figure 4. Numbers of ground beetle species per binary occupancy class (number of study sites occupied). White bars: observed numbers, grey bars: EDM, black bars: RAM. Errors denote one standard deviation. The three distributions are significantly bimodal ($p<0.05$ as inferred from the bimodality test of Tokeshi, 1992). Errors are one standard deviation.

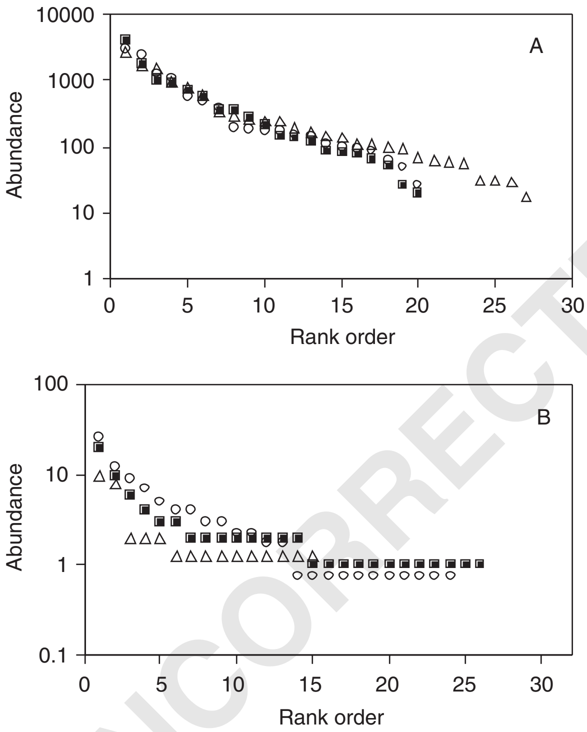

Figure 5. Rank–abundance distributions of the core (A) and satellite (B) species as defined by Fig. 4. Open triangles: RAM. Open circles: EDM. Black squares: observed species numbers. Note that in B ranks with equal abundances were transformed (abundance ± 0.25) to make the data points visible.

observed ones (Fig. 5). All observed data points of Figs. 5A and B ranged well within the 95% confidence limits of the respective EDM predictions (not shown in Fig. 5A to ensure readability). The SADs predicted by RAM instead deviated for core and satellite species from the observed pattern due to the higher number of core and the lower number of satellite species.

RAM not only predicted higher species numbers per island than observed. RAM also resulted in a significantly ($p(t)<0.05$) higher evenness D per island ($D_{\mathrm{RAM}}=0.89\pm0.002$) in comparison to the observed one ($D_{\mathrm{obs}}=0.79\pm0.04$) and to the EDM prediction ($D_{\mathrm{EDM}}=0.83\pm0.01$). Observed and EDM predicted evenness did not significantly differ ($p(t)>0.1$). Further, EDM predicted for core and satellite species an evenness similar to the observed one (core species: $D_{\mathrm{EDM}}=0.83\pm0.02$, $D_{\mathrm{obs}}=0.82$; satellite species: $D_{\mathrm{EDM}}=0.90\pm0.01$, $D_{\mathrm{obs}}=0.89$). RAM instead predicted a higher evenness for core ($D_{\mathrm{RAM}}=0.88\pm0.01$) and a lower evenness for satellite species ($D_{\mathrm{RAM}}=0.84\pm0.01$).

We analysed co-occurrence separately for core and satellite species and for species with different dispersal ability (Ulrich & Zalewski, 2006; Zalewski & Ulrich, 2006). RAM and EDM predicted for all of these groups a random spatial distribution of species (Table 1). Mean Z-transformed C-scores, checkerboard scores, and co-occurrence scores were in all cases within the boundaries ($-2<\mu<2$) expected from a standard normal distribution at the 5% error level (Table 1). Observed C-scores for core species and macropterous species instead indicated a strong spatial underdispersion (Z-transformed scores >3; Table 1 and Ulrich & Zalewski, 2006). The observed checkerboard and the co-occurrence scores that use absolute counts did not point to any deviation from a random spatial distribution.

Because for satellite species an analysis of nestedness is by definition impossible we studied nestedness only with regard to dispersal ability. As expected, RAM predicted for macropterous, brachypterous, and dimorphic species a nearly perfect nested pattern of island colonisation (Table 2). The matrix temperatures of the real data instead pointed to a much smaller degree of nestedness. That for macropterous species did not significantly differ (at $p<0.05$) from a random distribution. EDM predicted a pattern that was intermediate between the observed one and the RAM prediction (Table 1).

Discussion

The present results provide two main messages. First, island colonisation from a surrounding mainland is not a simple random draw of species from

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the common mainland pool. Our RAM model that only considered migration processes consistently overestimated the observed species numbers and the evenness per island (Fig. 2). It produced a higher number of core and a lower number of satellite species (Figs. 4 and 5). This result is of course in line with the classical theory of island biogeography that assumes island communities not only to be structured by colonisation processes but also by local extinction (MacArthur & Wilson, 1967). Our result can be compared with that of Dolman and Blackburn (2004), who found in their study of a British woodland avifauna that a random draw of species from the regional pool (the whole British fauna) is inferior to a local neutral model in predicting species numbers and local abundances. As in our study their random draw overestimated local species numbers and observed abundances.

EDM was not only able to reproduce correctly island species richness, SARs, and the AOD. Contrary to RAM it also predicted observed abundance distributions to a high accuracy (Fig. 5). Neutrality reduced total island species numbers with respect to the simple random draw and enhanced the numbers of satellite species. This indicates that local random extinction processes (due to death or emigration) act differently on core species that are mostly abundant overall and on satellite species that are mostly rare. Niche theory predicts a similar pattern in the case of competition structured communities (Chase & Leibold, 2003; Chave et al., 2002). Hence, our results corroborate earlier views that ecological drift and competition might result in similar abundance distributions making it very difficult to test both models (Harpole & Tilman, 2006; McGill, 2003a). The ultimate outcome of both models is similar: a reduction in local diversity and enhanced numbers of regionally rare species. Because locally rare species are also prone to regional extinction (Kunin & Gaston, 1997; Lande, Engen, & Saether, 1998) both processes might tend to decrease regional diversity.

Ecological drift did better than RAM in predicting multiple ecological patterns of site occupancy. Dolman and Blackburn (2004) obtained a similar result in their study on the species composition of a British woodland avifauna. They attributed their result to the additional birth/death rate parameter of their neutral model that allowed for a better fine tuning. Indeed, additional parameters of sufficiently flexible models should contribute to model fit. Nevertheless, it remains challenging for ecologists that a simple process like EDM with only two free parameters appears to be able to predict different distributions of species richness and abundances simultaneously.

Table 1. Observed C-scores, species combination scores, checkerboard scores and those obtained from 100 replicates of EDM and the RAM

Species group	C-scores			Species combination scores			Checkerboard scores		
	Observed value	Ecological drift	Random model	Observed value	Ecological drift	Random model	Observed value	Ecological drift	Random model
Core	6.5	−0.15±0.07	−0.21±0.14	0.5	−0.21±0.14	−0.32±0.02	0	0±0	0±0
Satellite	−0.36	−0.29±0.12	−0.15±0.18	0.3	−0.16±0.11	−0.34±0.02	−0.43	−0.47±0.08	0.16±0.12
Macropterous	3.09	−0.99±0.07	−0.74±0.08	0	−0.08±0.03	−0.06±0.01	1.11	0.17±0.08	0.03±0.04
Dimorphic	1.62	0.08±0.09	−0.21±0.11	0.34	−0.15±0.11	−0.03±0.13	−1.64	−0.13±0.09	0.05±0.03
Brachypterous	−0.7	−0.01±0.15	0.15±0.06	0.54	−0.06±0.09	−0.05±0.06	0.45	0.81±0.07	0.58±0.2

All scores are Z-transformed. Species groups as defined in the methods section.

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Table 2. Observed matrix temperatures *T* and those predicted by EDM and RAM for brachypterous, dimorphic, and macropterous species

Species group	Observed		EDM		RAM	
	T	T_{null}	T	T_{null}	T	T_{null}
Macropterous	31.4	38.3±4.1	16.4±4.1	44.1±5.7	5.6±0.9	54.4±5.9
Dimorphic	24.3	33.8±3.7	13.3±2.4	51.1±7.7	5.0±1.2	53.4±6.8
Brachypterous	8.5	24.5±5.5	15.7±3.9	29.7±13.5	2.4±1.4	28.0±11.1

T_{null} refers always to the associated randomized matrix temperatures generated by the nestedness temperature calculator. Standard deviations obtained from 100 replicates each.

However, there is also a growing list of counter-examples. For example, Adler (2004) failed to reproduce observed SAR and species–time relationship simultaneously. Harpole and Tilman (2006) reported that the abundance distributions within the grassland communities they studied were consistent with neutral theory while patterns of soil nitrate use were better explained by niche theory. These and other contrasting results regarding the fit to single distributions (for example Etienne, 2005; McGill, 2003a; Tuomisto, Ruokolainen, & Yli-Halla, 2003; Ulrich & Ollik, 2004; Volkov et al., 2003) call for a broader perspective in the discussion of neutrality which includes different aspects of community structure and different spatial and temporal scales (Adler, 2004; Chave, 2004; Harpole & Tilman, 2006; McGill, 2003b; Ulrich, 2004a).

The second main message from our results is that neither RAM nor EDM were able to mimic observed non-random patterns of species co-occurrences. In a previous paper one of us (Ulrich, 2004b) showed that neutrality leads—at least in species poor communities—to species co-occurrences that are not random but in line with the assembly rule model of Diamond (1975). Bell (2005) also showed that neutral models are able to predict a non-random pattern of species co-occurrences in plant communities, but that this ability depends on landscape structure, intensity of competition and survey design (study grain). Hence, our negative result shows that on our spatial scale and in the case of ground beetles (as opposed to probably less dispersive plants) EDM fails to mimic observed patterns of co-occurrence. These contrasting results again call for an analysis of on what scales and for what type of community neutral models are best suited (Adler, 2004; Chave, 2004; Hubbell, 2003; Gotelli & McGill, 2006; Harpole & Tilman, 2006).

Closely related to co-occurrence is nestedness. Nested communities are those that are perfect subsamples of the next larger ones (Atmar & Patterson, 1995). Indeed, RAM resulted in a highly nested pattern of site occurrences (Table 2). The observed matrix temperatures of dimorphic and macrocterous species predicted by EDM were significantly ($p(t)<0.01$) higher than those predicted by RAM and more close to the observed and to the null model expectation of randomness. Obviously, nestedness has not been studied yet in the context of ecological drift. Hence, from our single study it remains unclear whether our result with EDM predicting matrix temperatures intermediate between the observed ones and the RAM predictions can be generalised. If so, the study of nestedness might be an additional test whether and to what degree EDM is able to mimic observed patterns of site colonisation.

In general, our results show that neutral models can mimic patterns associated with species richness but have difficulties when dealing with patterns associated with species composition. They add further to the view that EDM is an appropriate null model for the study of ecological communities (Chave, 2004; Gotelli & McGill, 2006). Its ability to mimic basic patterns of biodiversity like SARs or AODs should sharpen our perception of niche differences and competitive effects that cause deviations from the model. As a null model EDM seems much better suited to distinguish between random effects and species interactions than simple random draw models.

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